

A new genus and species of freshwater mussel from the Pearl River Basin in Guangxi, China (Bivalvia, Unionidae, Gonideinae)

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Abstract

A new genus and species of freshwater mussels, *Guiunio rarus* Chen, Li, Dai & Wu, **gen. et sp. nov.**, is described from the Pearl River Basin in China based on comparative morphology and molecular phylogeny. The new taxon belongs to the tribe Gonideini and can be distinguished from other genera by a unique combination of characteristics: shell medium-sized, moderately thick, flat, long, sub-glossy, opaque; anterior small, rounded and short; posterior extremely expanded, wide and long, with an indistinct obtuse angle in the middle of posterior margin; papillae on flap margin highly degraded. The validity of it is further supported by the molecular phylogenetic analysis based on *COI*, *16S* and *28S* sequences.

Key Words

Biodiversity, molluscs, phylogeny, taxonomy

Introduction

Freshwater mussel is a group of large benthic animal that play an important role in freshwater ecosystems (Graf and Cummings 2007; Huang et al. 2019; Liu et al. 2022). China is a diversity hotspot of freshwater mussels, with about 100 accepted species recorded and new taxa continuing to be discovered (Heude 1875, 1877a, 1877b, 1878, 1879, 1880a, 1880b, 1881, 1883, 1885; Simpson 1900; He and Zhuang 2013; Graf and Cummings 2021, 2025; Guo 2022; Liu et al. 2022, 2023, 2024; Wu et al. 2021, 2022, 2024; Chen et al. 2023; Dai et al. 2023, 2024a, 2024b, 2024c, 2024d; MolluscaBase eds. 2025). The majority of studies on Chinese freshwater mussels are concentrated in the Changjiang River Basin (Yangtze) (Heude 1875, 1877a, 1877b, 1878, 1879, 1880a, 1880b, 1881, 1883, 1885; Zeng et al. 1981, 1985; Zeng and Liu

1989; Liu and Wu 1991; Wu et al. 1994, 1999, 2000, 2017, 2018, 2021, 2022; Shu and Wu 2004; Ouyang et al. 2011; Xiong et al. 2011, 2012; Xiao et al. 2012; Chen et al. 2023; Dai et al. 2024a, 2024d), with very few focusing on the Pearl River Basin (Dai et al. 2023, 2024b, 2024c; Liu et al. 2023, 2024; Wu et al. 2024). The Pearl River is the southernmost large river in China, located between the Changjiang River and the Red River. The recurrence of connectivity events throughout the history of the region has resulted in the fish community of the Pearl River Basin exhibited by both the local and the Changjiang River Basin's characteristics (Huang et al. 2017; Sun et al. 2022). However, the freshwater mussel community here remains a subject of limited knowledge due to the absence of systematic studies. Some sporadic studies have revealed the unique composition of freshwater mussels and several as yet undescribed species in the region (Dai

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et al. 2023, 2024b, 2024c; Liu et al. 2023, 2024; Hou et al. 2025). There are substantial regions here that have not yet been the subject of exploration and research.

Subfamily Gonideinae Ortmann, 1916, encompasses small to large freshwater mussels from East Europe, West Asia, East Asia, Southeast Asia, and North America (Graf and Cummings 2025; MolluscaBase eds. 2025). The shell morphology of the subfamily exhibits significant phenotypic plasticity and convergence, making it difficult to classify based solely on morphology reliably (Zieritz and Aldridge 2009; Inoue et al. 2013). China represents a diversity hotspot of the subfamily, harboring about 10 genera and 30 accepted species (Graf and Cummings 2025; MolluscaBase eds. 2025), and new taxa being discovered continuously (Wu et al. 2021; Dai et al. 2023, 2024a).

During the surveys in 2024, we discovered a group of freshwater mussel specimens with the special expanded posterior that did not resemble any known species and were challenging to place in any genus. Based on a combination of morphology and molecular phylogeny, we describe it as a new genus and species of subfamily Gonideinae. The discovery improved the diversity of freshwater mussels in the Pearl River Basin, leading to a more comprehensive understanding of the endemic species in the region.

Materials and methods

Specimens were collected from Guaangxi in China in 2024. Living specimens were initially frozen at -20 °C for 24 hours and subsequently thawed at room temperature for 2 hours to facilitate the extraction of soft parts. The soft parts were then fixed in 70% ethanol. Empty shells were cleaned, dried, and preserved at room temperature. Photographs were taken by camera and edited with Adobe Photoshop CC 2015 (Adobe, San Jose, US). Maps were made in ArcGIS Pro (Esri, Redlands, US).

Genomic DNA was extracted from foot tissues preserved in 70% ethanol using a TIANamp Marine Animals DNA Kit (Tiangen Biotech, China). The quality and concentration of the DNA were checked on 1% agarose gel electrophoresis and NanoDrop 2000 (Thermo Scientific, USA). Partial cytochrome c oxidase subunit 1 (*COI*), 16S ribosomal RNA (*16S*) and 28S ribosomal RNA (*28S*) were amplified and sequenced for molecular phylogenetic analyses. Polymerase chain reaction (PCR) systems, conditions and primer pairs were followed Dai et al. (2024a). The *COI* sequences were aligned using MEGA v. 6.0 (Tamura et al. 2013), and the *16S* and *28S* sequences were aligned using MAFFT v. 7 (Kato et al. 2019) by the Q-INS-i algorithm. The accession numbers of other species and newly obtained sequences are given in Table 1.

Phylogenies reconstructed by the dataset combined three genes using Maximum Likelihood (ML) and Bayesian Inference (BI). Five species of Unioninae Rafinesque, 1820 and Margaritiferidae Henderson, 1929 were used as the outgroups for rooting the trees. The best-fit model for

each gene and gene partition was calculated by Partition-Finder2 v. 1.1 (Lanfear et al. 2017), based on the corrected Akaike Information Criterion (AICc) and using a heuristic search algorithm. The program proposed the division of the concatenated dataset into three partitions, comprising partitions for the *16S* and *28S* genes and each of the three codon positions of the *COI* gene. The best-fit model was determined to be GTR+I+G for the first and second codon positions of *COI*, as well as for *16S* and *28S*, while GTR+G was selected for the third position of *COI*. ML analyses were performed in IQ-TREE v. 1.6.12 (Minh et al. 2013) using the Ultrafast bootstrap approach (Minh, et al. 2013) with 10,000 iterations. Bayesian inference (BI) analysis was conducted in MrBayes v. 3.2.6 (Ronquist et al. 2012). Four simultaneous runs with four independent Markov Chain Monte Carlo (MCMC) were implemented for 10 million generations, and trees were sampled every 10,000 generations with a burn-in of 25%. The convergence was checked with the average standard deviation of split frequencies <0.01 and the potential scale reduction factor (PSRF) ~ 1. Trees were visualized in FigTree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Abbreviations: NCU_XPWU: Laboratory of Xiao-Ping Wu, Nanchang University (Nanchang, Jiangxi, China); aam: anterior adductor muscle; pam: posterior adductor muscle; ea: excurrent aperture; ia: incurrent aperture; pia: papillae of the incurrent aperture; pea: papillae of the excurrent aperture; ig: inner gills; og: outer gills; m: mantle; lp: labial palps; vm: visceral mass; f: foot.

Results

Phylogenetic analyses

The sequence dataset consisting of 55 *COI*, 55 *16S* and 55 *28S* sequences from 50 species, including with five out-group taxa, was employed for phylogenetic analyses (Table 1). The alignments of *COI*, *16S* and *28S* genes had a length of 606, 516 and 457 characters, respectively. Within these alignments, 258, 235 and 168 sites were variable, and 238, 198 and 154 sites were parsimony informative. The Bayesian and Maximum Likelihood analyses produced same phylogenies (Fig. 1). The new species was sistered with genus *Cosmopseudodon* Haas, 1920 with relatively well support rate (BS/PP = 70/0.92).

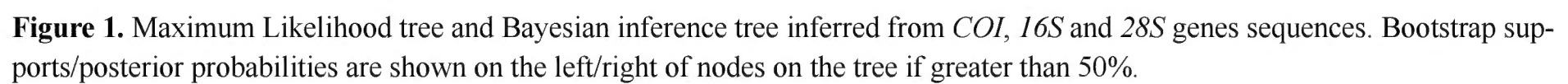
Systematics

Family Unionidae Rafinesque, 1820
Subfamily Gonideinae Ortmann, 1916
Tribe Gonideini Ortmann, 1916

Genus *Guiunio* Dai, Chen, Li & Wu, gen. nov.

<https://zoobank.org/8C80C6EF-3A7F-4568-8F8A-DC55228FE620>

Type species. *Guiunio rarus* Chen, Li, Dai & Wu, sp. nov.



Description. Shell medium-sized, moderately thick, flat, long, sub-glossy, opaque. Anterior small, rounded and short; posterior extremely expanded, wide and long, with an indistinct obtuse angle in the middle of posterior margin. Dorsal margin slightly curved downwards and truncated in behind; ventral margin weakly curved or retuse. Umbo inflated, slightly higher the hinge line, located at 1/4 of the dorsal margin, with concentric square carving. Periostracum

Table 1. Genbank accession numbers of sequences used in this paper.

Species	COI	16S	28S
UNIONIDAE Rafinesque, 1820			
Gonodeinae Ortmann, 1916			
Gonideini Ortmann, 1916			
<i>Guiunio rarus</i> gen. et sp. nov.	PV368601	PV368859	PV368862
<i>Guiunio rarus</i> gen. et sp. nov.	PV368602	PV368860	PV368863
<i>Guiunio rarus</i> gen. et sp. nov.	PV368603	PV368861	PV368864
<i>Obovalis omiensis</i>	MT020684	LC223994	MT020830
<i>Obovalis omiensis</i>	LC518995	LC223994	MT020830
<i>Obovalis omiensis</i>	LC518996	LC223995	LC519064
<i>Obovalis omiensis</i>	LC518997	LC519045	LC519065
<i>Ptychorhynchus pfisteri</i>	MG463036	KY067440	MG595564
<i>Ptychorhynchus pfisteri</i>	MG463034	KY067440	MG595563
<i>Ptychorhynchus pfisteri</i>	MG463035	KY067440	MG595562
<i>Parvasolenia rivularis</i>	MG463100	KX966393	MG595626
<i>Sinosolenia carinata</i>	MG463087	NC_023250	MG595616
<i>Sinosolenia oleivora</i>	MG463090	NC_022701	MG595617
<i>Sinosolenia iridinea</i>	MG463091	MT477834	MG595618
<i>Sinosolenia recognita</i>	MG463092	KY561653	MG595619
<i>Leguminaia wheatleyi</i>	MN402614	MN396725	MN396721
<i>Microcondylaea bonellii</i>	KX822652	KT966473	KX822609
<i>Gonidea angulata</i>	MN402615	MN396726	MN396722
<i>Koreosolenia sitgyensis</i>	MT020682	GQ451859	MT020817
<i>Postolata guangxiensis</i>	OP009379	OP020466	OP020470
<i>Postolata guangxiensis</i>	OP009380	OP020467	OP020470
<i>Postolata guangxiensis</i>	OP009381	OP020468	OP020470
<i>Postolata guangxiensis</i>	OP009382	OP020469	OP020471
<i>Postolata guangxiensis</i>	OP009383	OP020467	OP020472
<i>Postolata guangxiensis</i>	OP009384	OP020468	OP020470
<i>Postolata guangxiensis</i>	OP009385	OP020469	OP020471
<i>Postolata longjiangensis</i> *	PP786557	PP786405	PP786407
<i>Postolata longjiangensis</i> *	PP786557	PP786406	PP786407
<i>Postolata longjiangensis</i> *	PP786558	PP786405	PP786407
<i>Postolata longjiangensis</i> *	PP786558	PP786406	PP786407
<i>Pseudopostolata angula</i>	PQ189757	PQ201945	PQ201943
<i>Pseudopostolata angula</i>	PQ189757	PQ201945	PQ201944
<i>Cosmopseudodon resupinatus</i>	PP079436	PP079964	PP080006
<i>Cosmopseudodon wenshanensis</i>	PP079444	PP079972	PP080014

yellowish green to brown with thin growth lines. Posterior slope with an indistinct low secondary posterior ridge end in the angle on the posterior margin. Growth lines arranged in irregular concentric circles. Hinge long. Ligament short and strong. Beak cavities shallow, open. Mantle attachment scars on the pallial line obvious. Anterior adductor muscle scars irregularly oval, deep, smooth; posterior adductor muscle scars long oval, smooth. Left valve with two pseudocardinal teeth, posterior tooth elevated pyramidal or degenerated; anterior tooth thick and pyramidal. Right valve also with one pseudocardinal tooth, low triangular. Lateral teeth of both valves long and thin. Nacre light orange to white.

Mantle light brown, aperture margins black, papillae on flap margin highly degraded. Gills light brown, inner gills slightly longer and wider than outer gills. Labial palps-rown, distally pointed and irregularly fan-shaped in appearance. Visceral mass grayish white, foot light orange.

Species	COI	16S	28S
Pseudodontni Frierson, 1927			
<i>Pseudodon mekongi</i>	KX865861	KX865632	KX865733
<i>Pseudodon vondembuschianus</i>	KP795029	KP795052	MZ684028
<i>Pseudodon cambodjensis</i>	KP795028	NC_044112	KP795011
<i>Bineurus loeiensis</i>	KX865879	KX865650	KX865750
<i>Bineurus mouhotii</i>	KX865876	KX865647	KX865747
<i>Sundadontina tanintharyiensis</i>	MN275057	MN307248	MN307189
<i>Sundadontina brandti</i>	MN275058	MN307249	MN307190
<i>Pilsbryoconcha exilis</i>	KP795024	NC_044124	KP795007
<i>Pilsbryoconcha compressa</i>	KX865875	KX865646	KX865746
<i>Thaiconcha callifera</i>	KX865862	KX865633	KX865734
<i>Thaiconcha munelliptica</i>	MN275063	MN307252	MN307193
<i>Nyeinchanconcha nyeinchani</i>	KP795025	KP795050	KP795008
Lamprotulini Modell, 1942			
<i>Lamprotula caveata</i>	MG462991	NC_030336	MG595518
<i>Lamprotula leaii</i>	MN402616	MN396727	MN396723
<i>Potomida littoralis</i>	MN402617	MN396728	MN396724
<i>Pronodularia japonensis</i>	KX822659	AB055625	KX822615
Chamberlainiini Bogan, Froufe & Lopes-Lima in Lopes-Lima et al., 2017			
<i>Sinohyriopsis schlegelii</i>	MT020706	EF507846	MT020836
<i>Sinohyriopsis cumingii</i>	MG463086	NC011763	MG595613
<i>Chamberlainia hainesiana</i>	KX822635	NC_044110	KX822592
Rectidentini Modell, 1942			
<i>Hyriopsis bialata</i>	KX051274	MT993644	MT993697
<i>Ensidens ingallsianus</i>	MT993541	MT993687	MT993739
Contradentini Modell, 1942			
<i>Lens contradens</i>	MG581991	MT993693	MT993745
<i>Lens comptus</i>	KX865928	KX865682	KX865799
<i>Physunio superbus</i>	MG582020	MT993689	MT993741
Schepmaniini Lopes-Lima, Pfeiffer & Zieritz, 2021			
<i>Schepmania</i> sp.	MZ678755	MZ684082	MZ684035
Ctenodesmini Pfeiffer, Zieritz, Rahim & Lopes-Lima, 2021			
<i>Khairuloconcha lunbawangorum</i>	MN900790	MZ684078	MN902294
<i>Khairuloconcha sahanae</i>	MZ678752	MZ684079	MZ684024
Unioninae Rafinesque, 1820			
<i>Anemina arcaeformis</i>	NC_026674	NC_026674	MG595457
<i>Cristaria plicata</i>	NC_012716	NC_012716	MG595484
<i>Sinanodonta woodiana</i>	HQ283346	HQ283346	MG595604
MARGARITIFERIDAE Henderson, 1929			
<i>Gibbosula laosensis</i>	JX497731	KC845943	KT343741
<i>Margaritifera margaritifera</i>	KX550089	KX550091	KX550093

Etymology. The species is made from the *Gui* for the abbreviation for Guangxi and *unio* for the unionid type genus.

Vernacular name. 桂蚌属 (guì bàng shǔ).

***Guiunio rarus* Chen, Li, Dai & Wu, sp. nov.**

<https://zoobank.org/EE9A0840-BD0E-4568-9951-939B8E6D0DDF>

Fig. 2

Type material. *Holotype* • 25_NCU_XPWU_GR001, Zhongduhe River [中渡河], Luzhai County [鹿寨县], Liuzhou City [柳州市], Guangxi Zhuang Autonomous Region [广西壮族自治区], China, 24.60754°N, 109.80318°E, leg. Fan Li, January 2024.

Paratypes • n = 2, 25_NCU_XPWU_GR002–003, other information same as holotype.

Diagnosis. Same as the genus.

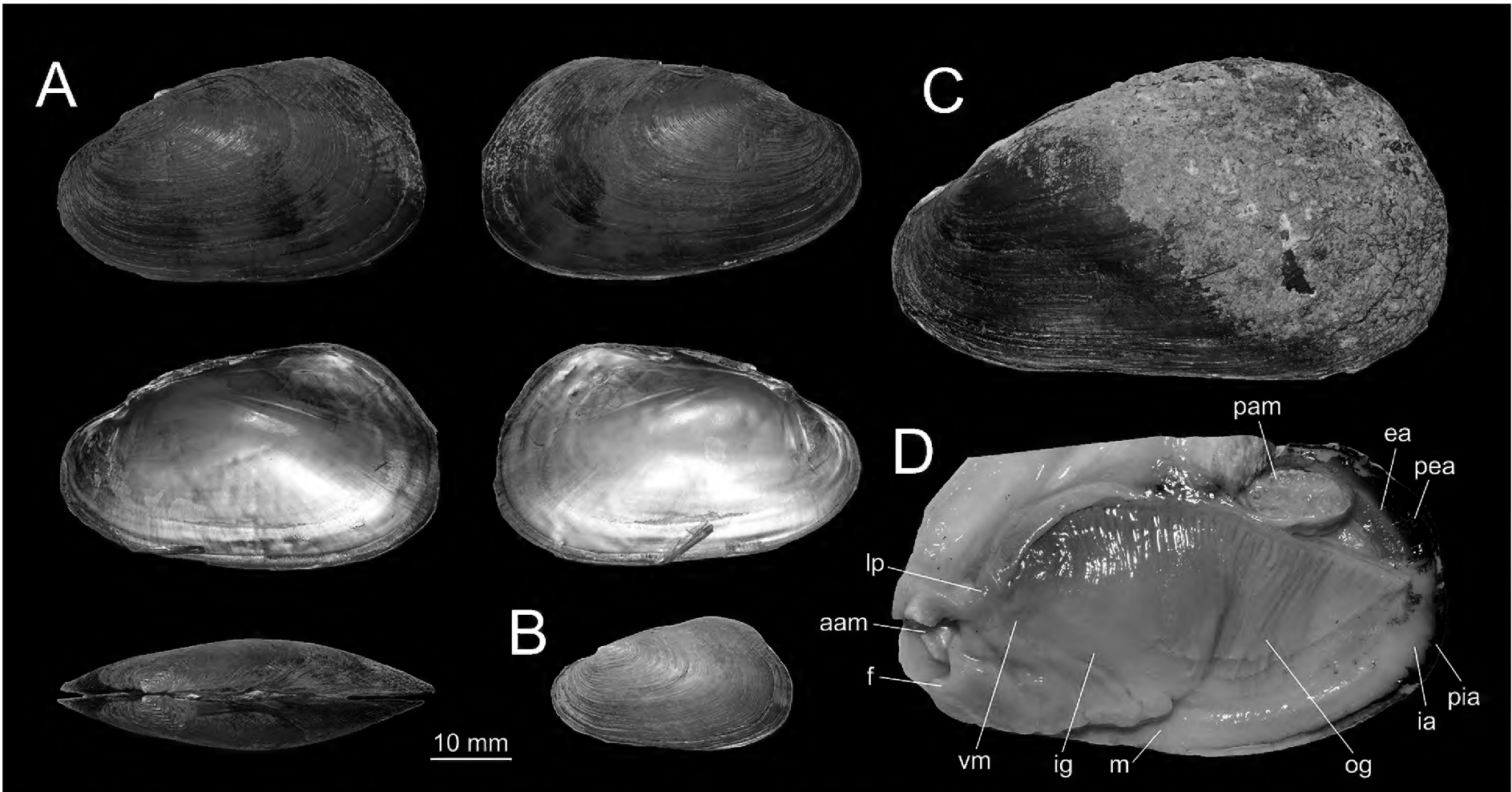


Figure 2. *Guiunio rarus* gen. et sp. nov. **A.** Holotype; **B, C.** Paratypes; **D.** Soft anatomy.

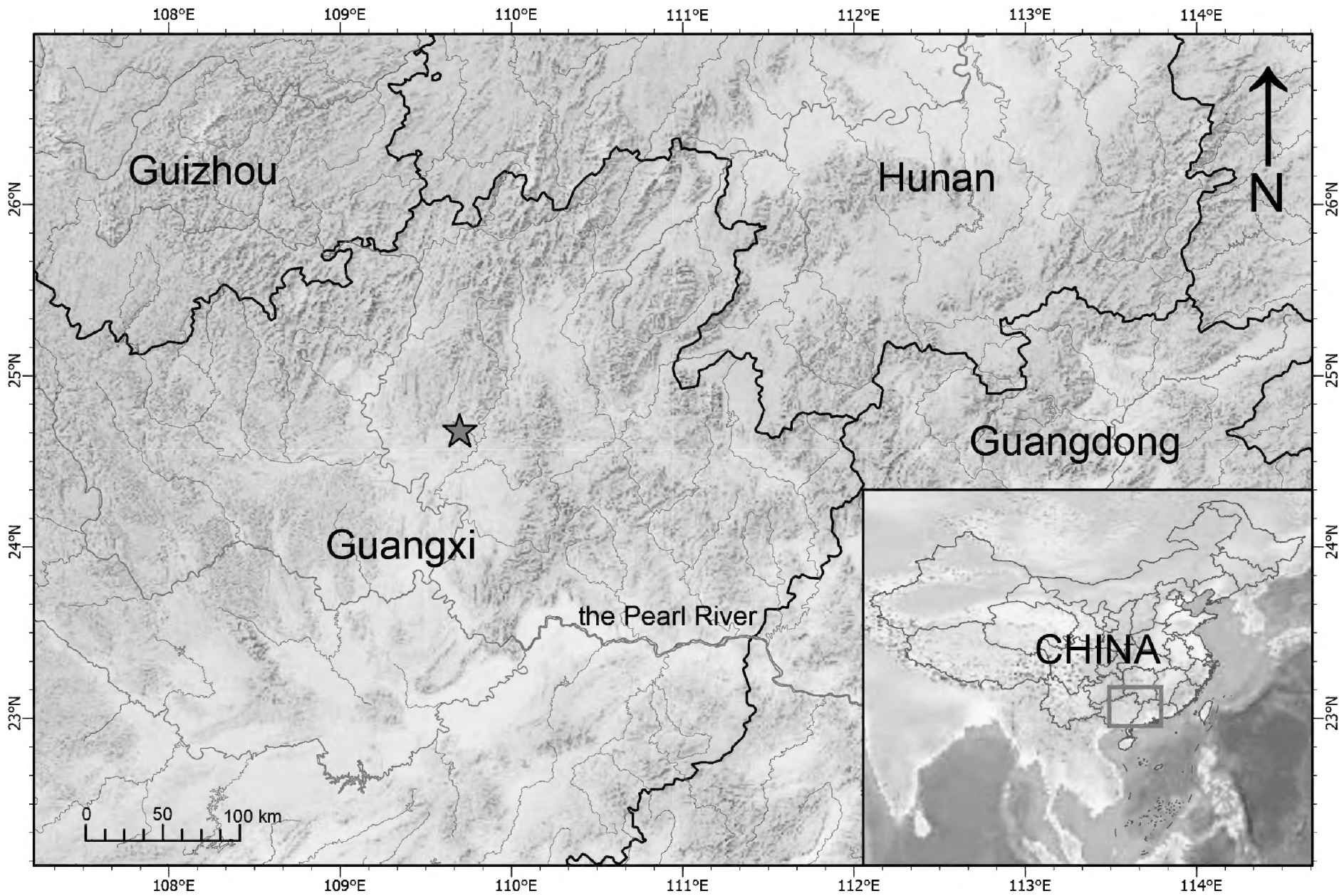


Figure 3. Distribution of *Guiunio rarus* gen. et sp. nov.

Description. Same as the genus.
Measurements. Holotype: shell length 50.0 mm, height 29.4 mm, width 14.2 mm. Paratypes: shell length 32.2–72.3 mm, height 18.1–42.2 mm, width 7.8–26.2 mm.
Etymology. The species is named after Latin *rarus* for rare, referring to the rarity of it.

Vernacular name. 稀有桂蚌 (xī yǒu guì bàng).
Distribution and ecology. Known from the type locality only (Fig. 3). Living in the slow flowing stream with muddy and sandy bottom alongside *Cristaria plicata* (Leach, 1814), *Nodularia douglasiae* (Gray, 1833) and *Lanceolaria gladiola* (Heude, 1877). In addition, the new

species was associated with a yet-to-be-described species of *Rhodeus* Agassiz, 1832, which may be laying eggs in the gills of it (all type specimens of the new species were collected during the dry season in winter, so no fish eggs were observed in the gills). It is an occasional species in the type locality, accounting for less than 1/20 of the population of all freshwater mussels.

Discussion

Despite the fact that only three type specimens were collected after an extended period of collection, molecular phylogeny and morphological comparison offer robust support for its independence. Molecular phylogenetic results supported placing the new genus in tribe Gonideini Ortmann, 1916. Within the tribe, the new genus is only similar to *Parvasolenia* Huang & Wu, 2019 by having an extremely expanded posterior, but differs by the thicker, opaque and sub-glossy shell (vs. thinner, semi-transparent and glossy shell), and the highly degraded papillae on flap margin (vs. with developed papillae on flap margin). The new genus was sistered with *Cosmopseudodon* in the phylogenetic tree, but differs by the extremely expanded posterior (vs. narrowed), the absence of an incision at the posterior (vs. presence) and the highly degraded papillae on flap margin (vs. with distinct papillae on flap margin). Within the subfamily, the new genus was similar to *Trapezoideus* Simpson, 1900, *Yaukthwa* Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019, and *Lens* Simpson, 1900 of tribe Contradentini Modell, 1942 by the similar shell shape, but differs by the oblique dorsal margin without developed wing, the more blunt posterior margin and the different distribution (southern China vs. Indochina). The convergent evolution of shell morphology among different groups in Unionida is a common phenomenon (Huang et al. 2018; Wu et al. 2020, 2022; Dai et al. 2024b), which may be attributable to adaptation to similar habitat environments.

The distribution of both the new species and a yet-to-be-described species of *Rhodeus* is confined to the same river, representing the second documented instance of sympatric occurrence between a new freshwater mussel and a new bitterling (Wu et al. 2022). Southern China is a hotspot for the both freshwater mussels and bitterlings (Guo 2022; Li 2025), and the special mutually beneficial symbiotic relationship between them may have driven their coevolution.

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